

XXVII.—*Some Thoughts on Subspecies and Evolution.*

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IN 'The Ibis' of this year, p. 345, appeared a letter over the signatures of Dr. Lowe and Mr. Mackworth-Praed, in answer to a letter of Mr. Loomis in 'The Ibis' of 1920, p. 965.

These letters bring out several points of great importance to those of us interested in evolution, distribution, and migration. These points can be enumerated as follows:—

1. Is intergradation necessary among forms in order to determine their status as species or as geographical races?
2. Is a geographical race due to one cause only—environment,—or can it be due to mutation? If the latter is the case, should they not be species?
3. Are geographical races incipient species, and can geographical races, whose differences are obviously due to environment, ever develop into a species?
4. Of what value is the subspecies?
5. Definition of a subspecies.

1. *Intergradation.*

Many eminent ornithologists have accepted the fact that absence of intergradation among birds results in a definite entity, the existing species, which must remain the only "definite minor unit in nature." This is probably correct and covers the vast majority of geographical races, but not all. Insular races, which are obviously but variations due to isolation, having no intermediate terrain with their parent stock, can naturally have no intermediate or intergrading races. The same argument applies to variations occurring among isolated continental communities, when the intervening country is unsuited to the life of the species. In these cases isolation is as complete as insular isolation, and the intervening range of hills, desert, or other obstacle

has no intermediate form, as suitable intermediate terrain does not exist.

It also seems that distance in isolation is of no consequence in permitting the union of two obvious geographical races under one species. We must all admit interrupted distribution, and who is going to define the limit of such interruption? A large number of New World and Old World forms have been united as geographical races of one species, even when no intermediate forms either do or can occur. If, then, we admit an interruption of 3000 miles, why not admit an interruption of 6000 miles or even greater distances?

If we were to accept the view that intermediate forms are essential for a true geographical race, we could not concede that a trinomial could be used except for purely environmental differences among contiguous races: neither could we allow that any isolated geographical race, showing purely environmental differences, is entitled to trinomial nomenclature.

It therefore appears that intermediate forms cannot be made an essential factor in determining a true geographical race, and that interrupted distribution, however extended, should not be a factor in rejecting an obvious geographical race.

2. *Causes of geographical variation.*

Lowe and Praed, whilst admitting that most geographical races are due to environment, consider that in some cases they are due to mutation. They challenge the whole Darwinian theory, and all principles of gradual evolution. They are not advocates of the "little by little" theory.

Let us examine Darwin's theory. It is ably summarised by Professor Punnett in his book on Mendelism. Darwin's theory briefly was:—

In any species of plant or animal the reproductive capacity tends to outrun the available food supply, and the resulting competition leads to an inevitable struggle for existence. Of all the individuals born, only a

portion, and that a very small one, can survive to produce offspring. The nature of the surviving portion is not determined by chance alone. No two individuals of a species are exactly alike, and among the variations which occur some enable their possessors to cope more successfully with the competitive conditions under which they exist. In comparison with their less favoured brethren they have a better chance of surviving and consequently of leaving offspring. Offspring tend to resemble their parents more than other members of the species, and favourable variations are transmitted.

In opposition to the Darwinian Theory is the Mutational Theory, which believes that new varieties suddenly arise from older ones by sharp sudden steps or mutations, and not by any process involving the gradual accumulation of minute differences. Such mutations turn up suddenly complete in themselves and are therefore "sports," their origin or meaning being unknown. Where such differences are due to a change in the gamete, they are heritable, are termed mutations, and are good species. Where such variations are not heritable, they are termed fluctuations and can never become permanent. Hybrids are, of course, mongrels, and no amount of selection, artificial or natural, can fix them as species.

Mutation is therefore regarded as the basis of all evolution, though it is conceded that the continued existence of a mutation is subject to natural selection.

Such is the theory based on Mendel's experiments and on the work of his many later disciples.

An examination of the experiments on which the Mendolian theories are based shows that they have been almost exclusively undertaken on plants and domesticated animals and under artificial conditions. In fact, they could not have been undertaken in any other medium. I believe that selection by man, and the perpetuation of sports or mutations as permanent varieties, whose differences are heritable, is a state which occurs but rarely in nature, and most of the deductions

from such experiments are of little value in studying evolution in its natural state. They are, of course, of immense value to the economist or poultry-fancier, but the artificial perpetuation of freaks is surely not a state of which Nature approves.

Natural selection works at the gradual improvement of life, and the elimination of what is not good, but has to work on certain definite material. Though I realise that every branch of life has great possibilities, there are equally very definite limitations. For instance, the struggle for existence precludes the various branches of life living as equals, certain groups always seeking leadership. When such accidents as mutational freaks occur, they spring into the world on their own responsibility, and are variations springing from within, being entirely divorced from environment. If the change is beneficial or harmless, they are allowed to remain and reproduce their freakish variation; if the change is harmful or a handicap, they die. When man, however, artificially perpetuates harmful freaks, he does so in spite of natural selection. So soon as man withdraws artificial protection and selection, the freak, thrown on the mercy of natural selection, must revert or perish. Such is the law for which we have to be thankful.

Moreover, it seems that nearly all artificially-produced races, when removed from artificial conditions, do not retain those variations which artificial selection has given them. The feral goats which I have seen in Ireland, Scotland, and on Round Island in the southern Indian Ocean, the feral Pigeon of Mauritius, and the Goldfish which after introduction to Madagascar devoured the only edible freshwater fish in the island, have all tended to revert respectively to wild Goat, wild Rock-Pigeon, and the ungainly mud-coloured ancestral stock of the Goldfish.

This leads me to assume that artificial selection does not (as Mendelians maintain) alter the gamete, unless artificial conditions and selection are maintained for a sufficiently long period to permit cumulative effect. But mutational variation under natural conditions remains constant, because natural conditions do not appreciably vary. But I admit that the

only cases of mutational variation which I can call to mind in nature are dimorphic forms, and it is by no means proved that such are mutational.

The mutationist will argue that whenever a domesticated variety resumes a wild life, the original wild stock being dominant to the recessive domesticated variety, such variety must revert, and that such a process is in strict accord with Mendel's theory.

But under natural conditions, constant variations, which unaided Nature has produced and which natural selection has perpetuated, do not revert. This still further convinces me that it is dangerous to apply to wild life the results of evolutionary experiments on domestic animals and plants. Both the experiments of Mendel and of more recent investigators have been conducted under conditions which do not exist in wild nature.

I would further mention that there is no artificial mutation which resembles any known variation separating natural species one from the other. Whether we take the domestic pigeon, fowl, or canary, it is remarkable that no single artificial variety has ever, so far as we know, occurred in a wild state.

I would also mention that natural selection, where environment remains unchanged, has no effect on evolution, except in those few cases of dimorphism which may or may not be mutational. But such an exception is pure theory.

I do, however, agree that in some cases natural selection may have allowed dimorphism, which is possibly mutational, to initiate a species. Such cases exist among the genus *Cyanthe*, in the Jackdaws (*Colæus dauricus* and *neglectus*), in the Skuas, and in many others. It appears that such mutants might establish themselves as good species, which would result in two species, separated by slight superficial differences, inhabiting the same area. Such a state at present exists among the Tree-creepers, Dippers, Rock-Nuthatches, the Whooper (*C. cygnus*) and Bewick's Swan (*C. bewicki*), and others.

But I cannot call to mind any geographical race which

can be ascribed to mutation. I believe they are all due to environment or isolation, both being geographical factors. A mutation has nothing whatever to do with geography.

I have tried to apply the mutation theory to species which contain undoubted geographical races. If I were to ask you to believe that mutation is responsible for geographical variation, I should have to ask you to believe that British races of Continental species all became smaller and darker quite suddenly and quite accidentally; I should have to ask you to accept that Egyptian Delta races all became dark by accident and spontaneously. I should have to ask you to believe that intermediate races in intermediate areas are accidental. You would have to swallow the fact that most pure desert species (*Alamon*, *Ammomanes*, *Pterocles*, *Eremophila*, *Ænanthe deserti*, *Cursorius*, and many others) are of the same sandy hue on their upper parts by accident, and are all descendants of "sports."

Take the Song-Thrush. The British race is darker than the Continental race. The Hebridean race is even darker than the British race. The degree of colour is in close relation to the degree of rainfall in the breeding-quarters of the three races. Is that accident? If so, similar remarkable accidents have occurred under similar conditions in many parts of the world, which would be preposterous to describe as a coincidence.

I shall not even attempt to convince you of such fallacies, as the theme is ridiculous. Evolution does not consist in the perpetuation of a series of defective freaks.

The advocate of mutation may say that such variations have proved of value to the bird, and have been perpetuated whilst other less suitable variations have been rejected by natural selection. But if that were the case, why does the Continental Song-Thrush spend from September to April in the British Isles, if the climate is so unsuited to its characters? And why do a host of other birds from the north spend the autumn, winter, and spring among their more southern representatives, if the area of the latter is so unsuited to the characters of the former?

The breeding-season is the most important period in a bird's life, and it is the environment of the breeding-area which influences variation more than winter-quarters. It is the fact that a bird like the Stonechat, which in various continental and insular forms breeds throughout Europe, Asia, and Africa, and many of whose races co-exist in the same winter-quarters, that induces me to believe that the environment or isolation of the breeding-quarters is in the main responsible for variation, and that this variation is the result of natural selection working on gradual change, and not the result of the perpetuation of some accidental and sudden freak.

I doubt very much whether mutation, or the sudden appearance of "sports," can establish a subspecies, though I believe a species might evolve another species by splitting, originating in mutation but eventually becoming a constant and heritable germinal character.

I also believe that wherever geographical races are connected by intermediate forms, it is absolute proof that the differences are entirely due to environment and not mutation, except where such intermediate forms are hybrids.

As a corollary to this, it follows that environment can affect the gamete; and this seems quite a reasonable assumption, if it is accepted that geographical causes influence the bird at all. Surely it is just as possible for the gamete to gradually change and enable new constant characters to become heritable, as it is for the gamete to suddenly change and embody heritable characters.

The mutationist will say that there is no evidence to show the gamete alters, and that, to perpetuate any environmental variation, the conditions to produce such variation must be repeated in each successive generation. In other words, acquired characters are not heritable.

That may be true for artificially-, accidentally-, or abnormally-acquired characters, but it is not true for environmentally-acquired characters, which are certainly heritable for one generation, but which appear to react to extremes of environment especially when artificially reproduced (*cf.* Beebe's experiment on Doves).

I would here draw attention to a valuable paper on "Inheritance of Acquired Characters" by Professor MacBride in the January number of 'Science Progress.' From experiments conducted by Kammerer on Salamanders and Midwife-Toads, it would appear that acquired characters are indeed heritable.

To sum up, I believe that nearly all evolution is the cumulative effect of environment, which acts with greater force and rapidity on isolated communities than on widely-distributed continental communities.

Weissmann, in his work on the Germ-Plasm, has been severely criticised for inferring that environment can directly influence the germ-cells without affecting the body-tissue in which the germ-cell is contained. This I believe to be partly correct, and I consider environment can affect the gamete to the following extent. If a European pays a visit to a tropical climate, his skin becomes tanned and brown under the influence of the sun's rays. The colour of his skin is naturally not transmitted to his offspring to any degree which is appreciable to the human eye. But if that same European settles in the tropics, the cumulative effect of the sun's rays on countless generations will permanently affect the colour of the skin by a very gradual process, and an eventual dark-skinned race will become established. I do not doubt that the germ-cell changes in exact proportion to the degree of permanence which cumulative environmental effect has on the body-tissue.

3. *Are geographical races incipient species?*

Where no isolation exists, geographical races will almost invariably be connected by intermediate forms in intermediate areas, and such intermediate areas may be but a mile or so in extent, or they may extend to a hundred miles or so; but such geographical races, when so constructed, can, in our opinion, never become species. It therefore follows that only isolated geographical races are incipient species, but to this end isolation must be complete.

We find many examples of this, the most remarkable being the case of the Chaffinch (*Fringilla cœlebs*). In the Canary Islands, as already pointed out by Bannerman (Ibis, July 1920), we find undoubted geographical races of the Chaffinch living alongside *Fringilla teydea*, and tending to vary in the same direction as a geographical race, as *F. teydea* does as a species. We believe that *F. teydea* was once but a geographical race of *F. cœlebs*, but that isolation has produced a species. The more recent invasions of Chaffinches to the Canary Islands are moving along the same path of evolution as did *F. teydea*, and are undoubtedly incipient species.

Though, therefore, we accept the fact that isolation produces a true species from an original geographical race, such can only occur under conditions of complete isolation. By far the majority of geographical races are not incipient species, and stand little chance of gaining that status so long as they are in actual touch with the parent stock.

I further wish to endorse the old truth that isolation is the strongest factor working for variation, and is the main factor in the evolution, not only of geographical races but of species.

4. *What is the value of a subspecies?*

We are not clear as to what is intended by this question. To him who asks what is the value of trinomial nomenclature, we reply that it has been found the shortest, most convenient and scientific way of referring to geographical variation. Its critics have not yet suggested a better way.

To him who asks of what value to science is the recognition of slight geographical variation, we reply that it helps to solve the problems of migration, evolution, and distribution among birds, and that such value has been recognised by the leading ornithologists of the world.

But there are still a few who regard the trinomial system as a simple and quick way of gaining notoriety, whilst others look on the method as a confusing and unnecessary invention of the Devil.

5. *Definition of a subspecies.*

There can be no hard-and-fast definition for a state of nature which is constantly changing. There exist forms which we all know, whose status is still unsatisfactory, and even Nature herself might have difficulty in defining them as species or subspecies, for the simple reason that they are in the transitional stage between the two.

But it seems correct to describe trinomially as geographical races those birds of similar type inhabiting different geographical areas, and whose differences are abundantly (not exclusively) constant within a given area. In fact, they must be a pure geographical variation, the variation coinciding with distribution.

Intermediate forms will nearly always be found in intermediate areas, but such need not always be the case, as in the instance of a race which has receded from its parent stock into temporary isolation, and which has again expanded towards its parent stock. Such appears to be the case with *Corvus f. frugilegus* and *Corvus f. pasinator*, and perhaps with *Erolia minuta* and *Erolia ruficollis*. Opinion is bound to differ regarding the status of such forms, as the question is a pure matter of opinion and not of fact.

Again, it is frequently stated that two geographical races of the same species must not breed in the same area. We agree that a geographical race is destroyed if another race of the same species continually breeds over a wide area of the former; but where two races of the same bird meet, they naturally, either by mating together or under the influence of intermediate conditions, produce intermediate forms. In fact, where this occurs it is good proof of the two races being good geographical races of the same species.

This short article is not intended to be a treatise on evolution. It has been written in the hopes that it may form the basis of a discussion in which we may have the opportunity to take part at some future meeting of the British Ornithologists' Club. To the highly-trained scientific mind, many of my contentions are no doubt ridiculous and untenable. It is the truth we seek, and if from the fallacies in my arguments others can point to more truthful causes of evolution, my time will not have been wasted.